

HYBRIDIZATION BETWEEN *CERCIDIUM FLORIDUM* AND *C. MICROPHYLLUM* (FABACEAE) IN CALIFORNIA

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ABSTRACT

Cercidium floridum A. Gray ssp. *floridum* and *C. microphyllum* (Torrey) Rose & I. M. Johnston (Fabaceae) hybridize where they have overlapping distributions in an area between Earp, and Parker Dam, CA. In this area, the two species have substantially overlapping blooming times, but are normally ecologically separated by habitat requirements with *C. floridum* ssp. *floridum* preferring the sandy washes and *C. microphyllum* preferring the volcanic rocky slopes of the Whipple Mountains immediately adjacent to the washes. The hybrids tend to be found only on the sandy terraces between the wash and the mountains or on the sand dunes in the area. The best diagnostic traits for distinguishing the parental species and their hybrids include leaflet length, banner petal width and color, legume shape in cross section, the degree of constriction between seeds in the legume, and the seed shape in cross section. Introgression from *C. microphyllum* into *C. floridum* ssp. *floridum* may be occurring, but there is presently only limited evidence of any reciprocal introgression. The taxonomic and evolutionary significance of hybridization between these two taxa is discussed.

RESUMEN

En un área entre Earp, California, y la represa Parker se han encontrado híbridos entre *Cercidium floridum* A. Gray ssp. *floridum* y *C. microphyllum* (Torrey) Rose & I. M. Johnston. Estas dos especies se encuentran separadas ecológicamente ya que el hábitat preferido por *C. floridum* ssp. *floridum* esta representado por lechos arenosos mientras que *C. microphyllum* prefiere las laderas montañosas de la cadena Whipple formadas por roca volcánica que bordean dichos lechos de río. Sin embargo, en esta zona la distribución de estas dos especies tienen una distribución superpuesta y además comparten un período de florecimiento común. Los híbridos se encuentran primordialmente en las terrazas arenosas localizadas entre las montañas y los lechos arenosos o en las dunas que se encuentran en el área. Los rasgos característicos más apropiados para distinguir entre las especies parentales y los híbridos incluyen el largo de las hojuelas foliolos, el ancho y color del pétalo central superior, la forma del corte transversal de la vaina, el grado de constricción la vaina entre las semillas, y la forma del corte transversal de la semilla. Aunque se observa una aparente introgresión de *C. microphyllum* en *C. floridum* ssp. *floridum*, evidencia introgresión recíproca es limitada. El significado entre la taxonomía y la evolución de hibridación de estas taxas se discuten.

While examining specimens of *Cercidium floridum* A. Gray ssp. *floridum* and *C. microphyllum* (Torrey) Rose and I. M. Johnston in the herbarium at Rancho Santa Ana Botanic Garden for a study of differences in ultraviolet (UV) floral patterns that act as a pre-pollination isolating mechanism (Jones 1978), we discovered a specimen collected by G. Wolf in 1940 that was annotated by him as a possible hybrid between these two species. The specimen (Wolf 9722, RSA) was collected about 11 miles (18 km) north of Earp, along the road to Parker Dam in San Bernardino County, CA. A field examination of this area in May 1972 revealed some interesting plants that had leaf characters that appeared to be intermediate between *C. floridum* ssp. *floridum* and *C. microphyllum*. The area was reinvestigated in April 1973 when both species were in full flower and we identified several possible hybrid individuals.

The vegetative and reproductive characters of the hybrids and their parental species have been described elsewhere (Jones 1978) and the parental

species have been discussed and described by Carter (1974a, b) and by Carter and Rem (1974). Carter (1974a), in her work on the genus *Cercidium* in the Sonoran Desert of Mexico and the Southwestern United States, indicated that she had found very few hybrids between *C. floridum* ssp. *floridum* and *C. microphyllum*. She cites only two herbarium specimens as examples, one of which was the *Wolf 9722* (RSA) and the other was *Kamb 2014* from Molina Crater, northwest of Sierra Pinacate in Sonora, Mexico. Because we had found several plants that appeared to be morphologically intermediate between these two species in the area around Earp, we decided to investigate the possibility that these individuals represented several additional examples of hybrids. Herein we describe our determination of these plants as hybrids based on distributional overlap and sympatry of the two parental species (Carter 1974a; Jones 1978), morphological intermediacy, ultraviolet floral pattern differences (as previously reported in Jones 1978), and reproductive potential as determined by pollen stainability,

TABLE 1. COLLECTION DATA FOR THE FIVE SAMPLE POPULATIONS OF *CERCIDIUM*.

Population	Taxon represented	# of plants sampled	Locality
1	<i>C. floridum</i> ssp. <i>floridum</i>	10	Base of the Whipple Mountains, adjacent to the Colorado River, 16.8 km north of Earp, on State Hwy. 62 toward Parker Dam, elevation 60.96 m, San Bernardino Co., CA.
2	<i>C. floridum</i> ssp. <i>floridum</i>	10	4.83 km south of the Iron Mountains, along north side of State Hwy. 62, elevation 610 m, Riverside Co., CA.
3	<i>C. microphyllum</i>	11	Same location as no. 1.
4	<i>C. microphyllum</i>	11	47.15 km south of Mexicali, Baja California, on Mex. Hwy. 5 near El Faro, in wash on side of road.
5	<i>C. floridum</i> ssp. <i>floridum</i> × <i>C. microphyllum</i> (hybrid)	12	Same location as no. 1.

seed germination, and artificial hybridization studies.

MATERIALS AND METHODS

Field studies were conducted during spring and early summer months from May 1972 through July 1976. Five populations were selected for study (Table 1) and every *Cercidium* plant within these populations was examined. The Earp populations (1, 3 and 5) were selected to represent sympatric individuals of *C. floridum* ssp. *floridum* and *C. microphyllum* and possible hybrids. Populations 2 and 4 were selected to represent allopatric individuals of the parental species. The distributions of the paren-

tal species and the locations of the population sites are shown in Figure 1. Herbarium specimens of the 54 plants analyzed from the five populations are deposited in the Faye A. MacFadden Herbarium (MACF) at California State University, Fullerton.

After an extensive examination of field samples and a careful review of the detailed descriptions and analyses provided by Carter (1974a, b) and Carter and Rem (1974), 12 quantitative and 13 qualitative characters were chosen for study (Table 2). Dial calipers, accurate to 0.01 mm, were used to make the 12 quantitative measurements illustrated in Figure 2. Five measurements per plant were taken for each quantitative character. Ultraviolet floral patterns were determined using techniques described by Jones (1978). Student's t-tests or one-way ANOVA were completed to determine if significant differences exist between character states in allopatric versus sympatric populations. Variation in the morphological characters for all plants from the five populations were analyzed graphically using a pictorialized scatter diagram and we used the hybrid index technique (Anderson 1949) to determine which plants to use for our artificial crosses. Characters and index values assigned to each are presented in Table 2.

Nectar samples taken from both parental types and the hybrids were sent to Drs. Irene (now deceased) and Herbert Baker at the University of California, Berkeley for analysis.

Pollen viability was estimated for each sample plant by staining the pollen with Cotton Blue (1% aniline blue in lactophenol) for at least 24 hours. Pollen from at least five separate flowers for each plant was used and a minimum of 400 grains were counted per plant. Those grains that stained dark blue and were of normal size and shape were considered viable, whereas those that stained faintly or not at all or were misshapen were considered inviable (Lawrence 1963).

Seeds were collected from every plant sampled. At least 100 seeds from each plant were scarified by soaking in concentrated sulfuric acid for three

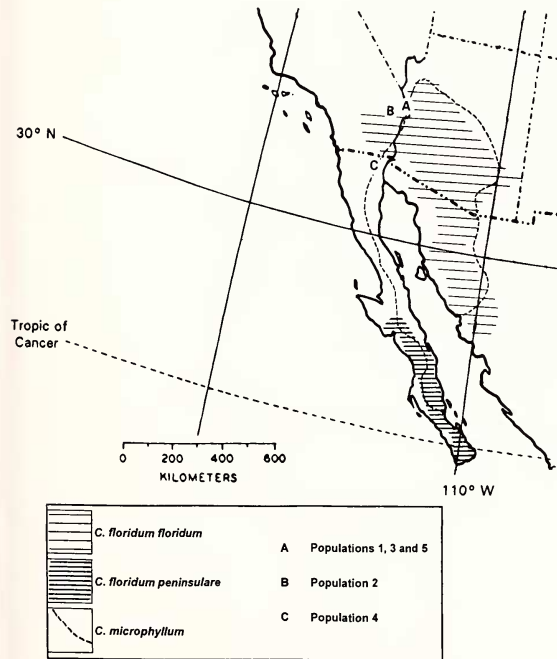


FIG. 1. Study sites and distribution of *Cercidium floridum* ssp. *floridum*, *C. floridum* ssp. *pensulare* and *C. microphyllum*. Map based on Carter (1974a).

TABLE 2. COMPARATIVE CHART OF MORPHOLOGICAL CHARACTERISTICS ILLUSTRATING THE INTERMEDIACY OF THE PUTATIVE HYBRIDS BETWEEN *CERCIDIUM FLORIDUM* ssp. *FLORIDUM* AND *C. MICROPHYLLUM*. The mean and the range, in parentheses, are given for each quantitative character. Characters used to construct the morphological hybrid index are indicated with an asterisk. Values assigned to the hybrid index characters are zero (0) for *C. floridum* ssp. *floridum*, two (2) for *C. microphyllum* and one (1) for the intermediate state.

Hybrid index value	<i>C. floridum</i> ssp. <i>floridum</i>	Hybrid	<i>C. microphyllum</i>
Character	0	1	2
Branchlet tips*	without spinescent tips	variable	spinescently tipped
Branchlet surfaces*	glabrous	variable	pubescent
Axillary spines*	present	present or absent	absent
Branch color*	blue-green	green to yellow-green	yellow-green
Leaflet color*	blue-green	green to yellow-green	yellow-green
Banner petal color*	yellow	cream	white
Banner petal orange dots*	present	present or absent	absent
Ovary*	glabrous	variable	pubescent
Apex of legume*	broadly acute	intermediate	long acuminate
Pod shape*	flattened	somewhat rounded	rounded
Fruit*	not constricted between seeds	intermediate	constricted between seeds
Seed shape*	oblong, flattened	intermediate	elliptic, rounded
Leaflets, # of pairs*	2.8 (2-4)	3.6 (2-5)	6 (5-9)
Leaflets, length (mm)*	4.1 (2.0-7.0)	3.3 (1.8-6.0)	1.6 (0.05-2.5)
Banner petal length (mm)	11.9 (9-15)	11.1 (8-14)	8.7 (4-10)
Banner petal width (mm)*	9.5 (7-12.5)	7.3 (4-14)	4.9 (3.1-7)
Flower diameter (mm)*	22.5 (18-26)	20.2 (16-27)	16.0 (12-21)
Anther length (mm)	2.0 (1.5-2)	2.1 (1.9-3)	2.0 (1.8-2.2)
Rachis length (mm)	27.7 (14-45)	22.1 (11-35)	31.1 (12-52)
Sword length (mm)	9.0 (3-19)	14.1 (4.5-37)	16.3 (7-34)
Length of pedicel, base of sepals to abscission layer (mm)*	3.3 (1.5-5.5)	2.1 (1.5-4)	1.5 (1.0-3)
Length of pedicel, abscission layer to rachis (mm)	7.0 (4-10)	7.1 (4.5-14)	5.0 (3-8)
Seed length (mm)	10.3 (8.8-12.2)	9.8 (8.2-12.4)	9.2 (7.0-11.9)
Seed width (mm)	7.2 (5.1-8.4)	6.5 (5.3-8.2)	6.4 (5.4-7.6)
Seed thickness (mm)	3.9 (3.3-4.9)	4.0 (3.1-5.1)	4.9 (3.9-6.1)
Pollen stainability (%)	77.4 (39-97)	77.3 (54-93)	85.7 (21-98)
Seed germination (%)	83.8 (58-100)	84.7 (46-99)	80.7 (32-96)

hours, then rinsed with distilled water and planted in small plastic pots filled with standard potting soil mix. The percent germination was calculated for each plant.

Artificial crosses were conducted in the field using pollinator exclusion bags from Wards (Wards No. 20W-7300, which are no longer available). Both crosses between the parental species and backcrosses to the putative hybrid were attempted. Branches having numerous unopened floral buds were bagged and the buds allowed to open. Flowers to be used as the female parent, or pollen recipient, were emasculated in the bud. Pollination was accomplished by removing pollen from mature anthers with a dissecting needle and placing it on the stigma of an emasculated flower. After pollination, the pollinator exclusion bags were replaced. The bags were periodically examined and all fruits that developed were harvested at maturity. The seeds from these crosses were treated, and percentage germination was determined, as described for the wild-collected seed.

RESULTS

Comparative morphology. Twenty-two of the 25 morphological characteristics studied (Table 2) were shown to be of some value in the delineation of the parental taxa and in the establishment of the intermediacy of their hybrids. However, certain characters such as leaflet length, banner petal width and color, legume shape in cross section, the degree of constriction between seeds in the legume, and seed shape in cross section proved to be more diagnostic.

Analysis of population samples. Variation exhibited in allopatric and sympatric populations of the parental species is represented in Figure 3. Squares represent allopatric individuals of each parental species, and circles represent sympatric individuals of each. Group (A) represents *C. microphyllum* (populations 3 and 4) and Group (B) represents *C. floridum* ssp. *floridum* (populations 1 and 2). Based on the morphological characteristics employed in this study the two species are quite distinct, al-

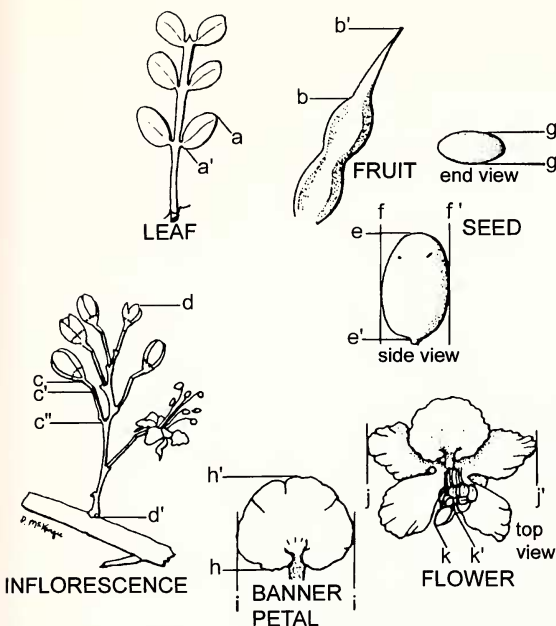


FIG. 2. Quantitative measurements of morphological characteristics as follows: a-a', leaflet length; b-b', legume sword length; c-c', length of pedicel from base of sepals to abscission layer; c-c'', length of pedicel from abscission layer to rachis; d-d', length of rachis; e-e', length of seed; f-f', width of seed; g-g', thickness of seed; h-h', length of banner petal; i-i', width of banner petal; j-j', diameter of flower; and k-k', length of anther.

though there is greater range of variability in *C. floridum* ssp. *floridum* in most of the quantitative characteristics analyzed than in *C. microphyllum*. The differences between the allopatric and the sympatric populations of *C. floridum*, ssp. *floridum* as reflected in Figure 3 and based on leaflet length and banner petal width, are in marked contrast to the lack of variation between the allopatric and the sympatric populations of *C. microphyllum*. Using a Student's *t*-test, the leaflet length is significantly different at the 0.05 level ($t = 2.78$, $df = 9$) when the allopatric and the sympatric populations of *C. floridum* ssp. *floridum* are compared. Significant differences were not found when a comparison of allopatric and sympatric populations of *C. microphyllum* was completed.

Similar influence of *C. microphyllum* on *C. floridum* ssp. *floridum* in sympatry is exhibited in banner petal length (comparison of allopatric vs. sympatric populations of *C. floridum* ssp. *floridum* were significant ($P = 0.05$, $t = 2.38$, $df = 9$). Although not significant at the 0.05 level, the diameter of the flowers showed a similar trend.

In Figure 4, leaflet length and banner petal width are plotted for the hybrids, (represented by triangles) along with the parental types. This figure clearly demonstrates the intermediacy, in leaflet length and banner petal width, of these hybrids between the parental species.

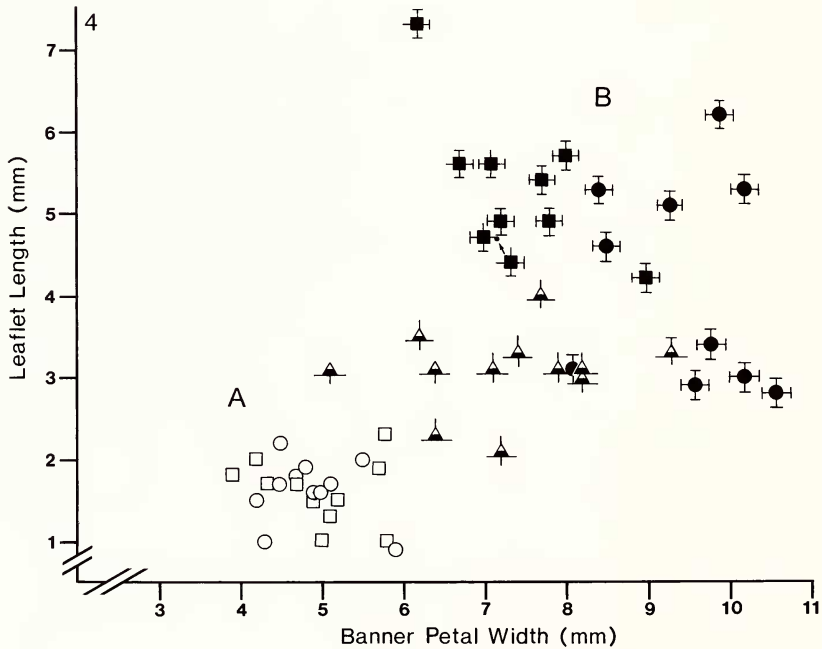
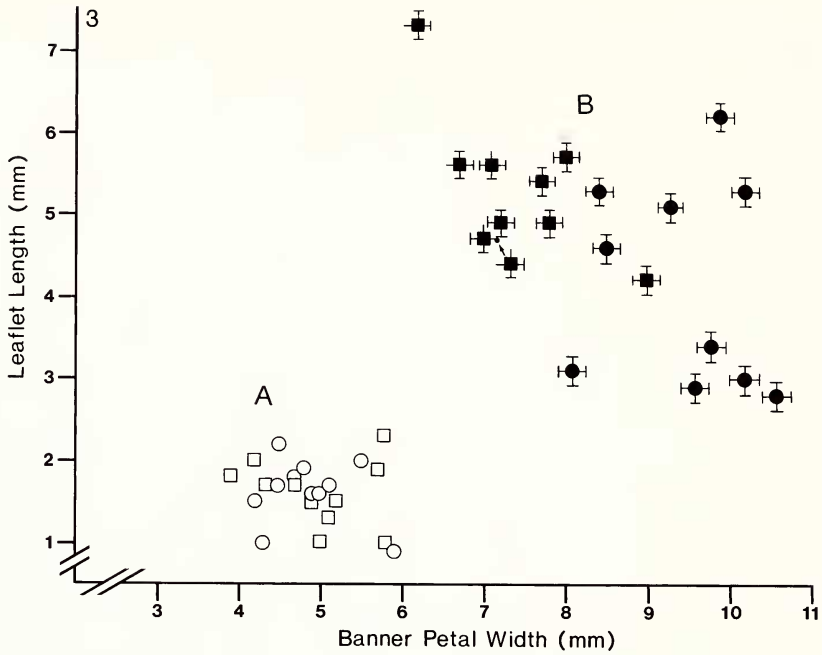
Nectar analysis. Table 3 summarizes the analysis of the nectar from both parental species and a putative hybrid. These data indicate that in amino acid content the putative hybrid sampled (# 1016) is identical to the plant of *C. microphyllum* sampled (# 4010). *Cercidium floridum* ssp. *floridum* differs in lacking lysine and tryptophan and in having a somewhat reduced concentration of threonine. In sugar content, the putative hybrid has more fructose and glucose, but considerably less sucrose than either parental species.

Fertility, experimental crosses and seed germination. The range and average pollen stainability and seed germination for both parental species and the hybrids were so similar that no statistical tests were done. These results are included in Table 2. All of the F_1 and backcrosses attempted between *C. floridum* ssp. *floridum* and *C. microphyllum* or their hybrid produced viable seed. The results of attempted crosses are presented in Table 4. The hybrid index value (HI) is given for each parent and the pollen stainability is reported for the male parent in each cross.

DISCUSSION

Cercidium floridum ssp. *floridum* and *C. microphyllum* have many obvious distinguishing characters (Carter 1974a; Carter and Rem 1974; Jones 1978; Siemens et al. 1994), illustrated in Figure 5, including size and number of leaflets; position and size of branch spines; size and coloration of flower parts; degree of constriction between seeds in fruits; and shape, size, and color patterns of seeds. The hybrids tend to be intermediate in most of these characters (see also Siemens et al. 1994).

It should be noted that some of the variation in flower color attributed to *C. microphyllum* in previous studies (Carter 1974a, p. 48) is probably due to post-pollination changes in banner petal color and is not typical of unpollinated flowers. Carter (1974a) notes, "Flowers of *C. microphyllum* differ also in having the limb of the long-clawed upper petal [banner petal] white, or occasionally cream or pale yellow . . ." Upon completion of pollination, the flowers of both *C. microphyllum* and *C. floridum* ssp. *floridum* undergo significant changes in floral color or symmetry that result in these flowers no longer being visited by the pollinating bees. In *C. microphyllum*, the change in banner petal color from white to cream or even yellowish is the result of a simple pH change. This change was duplicated by placing white banner petals in a weak sodium hydroxide solution and was reversed by immersing these treated petals in a weak solution of hydrochloric acid. In *C. floridum*, ssp. *floridum* on the other hand, the color of the banner petal does not change, but the banner petal folds down over the stamens, thus changing the symmetry of these spent flowers. This latter type of post-pollination change was previously reported for *Caesalpinia eriostach-*



○ plants from allopatric pops 2 and 4	Seed shape in cross section	Legume shape in cross section
□ plants from sympatric pops 1 and 3	○ rounded	○ rounded
△ hybrids, pop 5	◌ intermediate	◌ somewhat rounded
	◌ flattened	◌ flattened
Banner petal color	Apex of legume	Fruit constriction between seeds
○ white	○ long, acuminate	○ constricted
◐ cream	◌ intermediate	◌ somewhat constricted
● yellow	◌ broadly acute	◌ not constricted

TABLE 3. A BREAKDOWN OF THE MAJOR COMPONENTS OF THE NECTAR OF *CERCIDIUM MICROPHYLLUM*, *C. FLORIDUM* ssp. *FLORIDUM* AND THEIR PUTATIVE HYBRID. + indicates presence, ++ indicates abundance, +/- indicates traces and - indicates absence. ¹ Osmic acid test. ² 2-6 dichlorophenol-indophenol test. ³ Dragendorff test. ⁴ Brom-phenol test. ⁵ p-nitrovaniline test.

Collection no.	<i>C. microphyllum</i>	Hybrid	<i>C. floridum</i> ssp. <i>floridum</i>
	4010	1016	4011
Sugars			
Fructose	16%	27%	22%
Glucose	25%	32%	23%
Sucrose	59%	37%	50%
Maltose	—	4%	5%
Amino acids			
mg/ml	1.17	1.17	0.78
Alanine	+	+	+
Arginine	++	++	++
Asparagine	+/-	+/-	+/-
Aspartic acid	+	+	+
Glycine	++	++	++
Histidine	++	++	++
Lysine	+	+	-
Proline	+	+	+
Serine	++	++	++
Threonine	++	++	+
Tryptophan	+	+	-
Lipids ¹	+	+	+
Antioxidants ²	-	-	-
Alkaloids ³	-	-	-
Protein ⁴	+	+	+
Phenolics ⁵	deep yellow	deep yellow	pale yellow

ys (Jones and Buchmann 1974). In the hybrids, the banner petal in some flowers folds down over the stamens; and in other flowers, on the same plant, it stays erect and changes in color from cream to yellowish.

As noted in Jones (1978), the two parental species differ in corolla size and in their response to ultraviolet light. The petals and stamens of the small-flowered *Cercidium microphyllum* are entirely absorbent, whereas only the banner petals and stamens of the large-flowered *C. floridum* ssp. *floridum* absorb UV while the lateral petals are reflective. The hybrid plants display large corollas similar to those of *C. floridum* ssp. *floridum* but the flowers are entirely absorbent (Fig. 5).

Although not considered in this paper, it should be pointed out to other taxonomists who might consider the use of UV floral patterns as a taxonomic characteristic, that such patterns, if determined from herbarium specimens and depending on which flavonoid pigments are involved in the UV absorp-

tion portion of the pattern, may change when the flowers are dried. These changes appear to commonly occur when the UV absorbing pigments are anthochlors (Scogin, Young, and Jones 1977). Since anthochlor pigments are known to be associated with UV floral patterns in the genus *Cercidium* (Hiegel and Jones unpublished), caution should be exercised in making taxonomic judgments based on these traits; such changes can result in spurious variation. When extensive variation in UV floral patterns is detected from herbarium specimens, such as Carter (1974b) found in *Cercidium praecox* and *C. sonora*, a thorough investigation of living material should be undertaken to determine if such variation exists in living plants.

The flowers of *C. floridum* ssp. *floridum* have smaller banner petal widths when in sympatry with *C. microphyllum* and more closely resemble those found in *C. microphyllum*. The differences found in the banner petal width of *C. floridum* ssp. *floridum* collected from different populations may be

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FIG. 3. Pictorialized scatter diagram for *Cercidium* populations 1-4. Grouping (A) represents *C. microphyllum* and (B) *C. floridum* ssp. *floridum*.

FIG. 4. Pictorialized scatter diagram for *Cercidium* populations 1-5 with hybrids plotted as triangles. Key to symbols the same as in Fig. 3.

TABLE 4. RESULTS OF ARTIFICIAL CROSSES ATTEMPTED BETWEEN *CERCIDIUM FLORIDUM*, *C. MICROPHYLLUM* AND THEIR PUTATIVE HYBRIDS. * +Female parent is listed first. ** Fruits and seeds eaten by rodents.

Taxa	Female parent		Male parent		% pollen stainability	# flowers pollinated	# fruits developed	# seeds produced	Percent germination
	Coll. #	HI	Coll. #	HI					
<i>C. floridum</i> * × <i>C. microphyllum</i>	1020	4	1019	33	97.5	57	2	3	—**
<i>C. floridum</i> × <i>C. microphyllum</i>	5011	5	5012	33	93.0	35	9	17	81.3
<i>C. floridum</i> × hybrid	1020	4	1018	15	91.5	41	5	8	62.5
<i>C. floridum</i> × hybrid	5011	5	5010	18	74.0	16	1	1	0.0
Hybrid × <i>C. floridum</i>	5010	18	5011	5	71.5	58	3	4	50.0
Hybrid × <i>C. floridum</i>	1018	15	2011	2	96.5	23	4	6	—**
Hybrid × <i>C. floridum</i>	2010	19	2011	2	96.5	19	1	0	—
Hybrid × <i>C. microphyllum</i>	2010	19	1019	33	97.5	29	4	7	42.9
Hybrid × <i>C. microphyllum</i>	5010	18	5012	33	93.0	21	3	5	60.0
<i>C. microphyllum</i> × hybrid	1019	33	2010	19	85.5	24	2	3	33.0
<i>C. microphyllum</i> × hybrid	5012	33	5010	18	74.0	37	6	8	50.0
<i>C. microphyllum</i> × <i>C. floridum</i>	1019	33	2011	2	96.5	32	6	9	44.4
<i>C. microphyllum</i> × <i>C. floridum</i>	5031	32	5001	5	81.0	17	2	3	66.7

best attributed to the influence of *C. microphyllum* on *C. floridum* ssp. *floridum* as mediated through the hybrids. The differences in leaflet length might be attributed to habitat moisture differences between the allopatric and the sympatric populations of *C. floridum* ssp. *floridum*, which were not present in *C. microphyllum* populations. *Cercidium floridum* ssp. *floridum* exhibits an ecological preference for desert washes, whereas *C. microphyllum* tends to be found up out of the washes on the plains or hillsides (Carter 1974a; Jones 1978). The sympatric site (population 1) for *C. floridum* ssp. *floridum* is along the Colorado River and although no exact quantification was undertaken, these washes appear to be more mesic than the washes where the allopatric population of *C. floridum* ssp. *floridum* (population 2) was sampled.

Although there is no evidence of hybrid *Cercidium* progeny successfully outcompeting the parental species in the sympatric zone in California (Jones 1978), the differences in floral morphology described above suggest the remote possibility of introgression through the hybrids of *C. microphyllum* and *C. floridum* ssp. *floridum* (see also Siemens et al. 1994). This interpretation, although the antithesis of an earlier study (Jones 1978), is supported by the observation that the peak flowering of the hybrids shows greater synchronism with *C. floridum* ssp. *floridum* than with *C. microphyllum*. This greater synchronism of flowering seems to be

of greater importance than the fact that the hybrid and *C. floridum* ssp. *floridum* have distinct UV and visible floral patterns.

The sugars, amino acids, and other components present in the nectar of the hybrid appear to represent simply a summation of those present in the two parental species (Baker and Baker 1976). The hybrid resembles *C. microphyllum* in amino acid and phenolic content but presents novel proportions of the simple sugars, and the presence of maltose reveals the genetic contribution of *C. floridum* ssp. *floridum*. Further evidence of hybridization was demonstrated by Siemens et al. (1994) using two-dimensional flavonoid spot patterns of both species and hybrids.

Viable seed can be produced from interspecific crosses involving *C. floridum* ssp. *floridum* and *C. microphyllum* and from artificial backcrosses (Table 4). It is of interest to note that although there is little evidence of any influence of backcrossing on *C. microphyllum*, such backcross progeny are possible. In both parental species and the hybrids a large range of pollen stainability percentages was encountered. This may indicate an otherwise cryptic influence of introgression on *C. microphyllum*, as well as further evidence for backcrossing between *C. floridum* ssp. *floridum* and the hybrids, because most of the lower pollen stainability counts were derived from sympatric individuals of the two parental species.

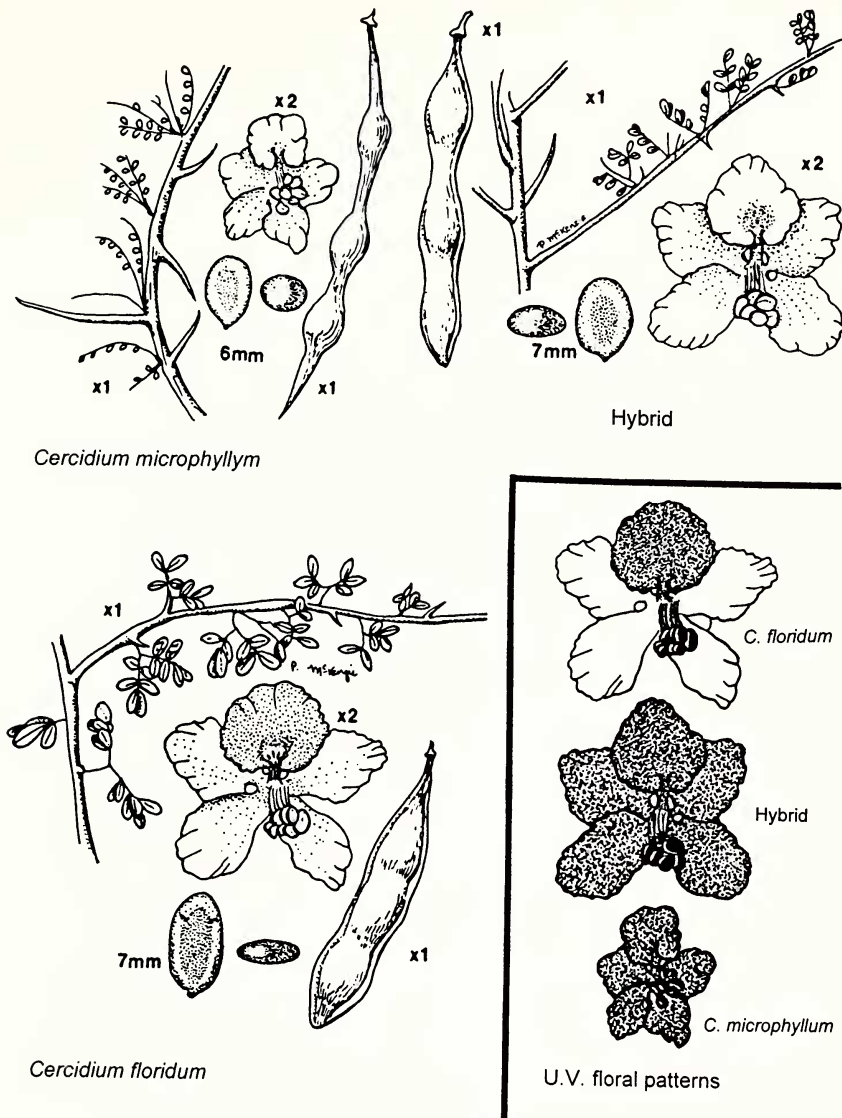


FIG. 5. Distinguishing characteristics of *Cercidium floridum* ssp. *floridum*, *C. microphyllum* and their hybrid.

Hybridization between *C. microphyllum* and *C. floridum* ssp. *floridum* either is an uncommon event or environmental pressures prevent the hybrids from becoming established in greater numbers. The average frequency of hybrids found in the various populations studied in the area of sympatry in California was only 3.2% (range 1.0–9.97%). This frequency of hybrids is particularly low given that these species are long-lived perennials living up to 400 years in age (Benson and Darrow 1944). Although the frequency of hybrids compares favorably with the frequency of “mistakes” made by pollinating bees in areas of sympatry (Jones 1978), it should be emphasized that in species with such slow replacement rates, minor differences in ecological requirements exhibited by these two species may result in significant selective pressures for the

maintenance of certain genotypes in the population. As a result of such pressures, even fertile hybrid progeny would be eliminated from all but the rather extensive, naturally disturbed, floodplain, intermediate habitats. Most of the hybrids were found in this habitat. This may help explain the very cryptic evidence of introgression found in the population of *C. floridum* ssp. *floridum* that was sympatric with *C. microphyllum*.

Although our work has substantially increased the knowledge about the number of known, naturally-occurring hybrid progeny between *C. floridum* ssp. *floridum* and *C. microphyllum*, it appears that hybridization is limited to some peripheral sympatric zones; and as such is probably of little evolutionary consequence for these species. However, it would be of interest to thoroughly examine other

zones of sympatry to see if hybridization is occurring. For example, the specimen collected by Kamb (*Kamb 2014*) and cited by Carter (1974a) as a hybrid from Sonora, Mexico, would serve as a start for more detailed studies on the extent over the vast area of sympatry of these two species. A collection trip in 1997 revealed another possible area of hybridization, between Quartzite, AZ and Blythe, CA where individuals of both species were simultaneously in bloom. Isozymic studies of the two parental species and their hybrids are currently underway and we anticipate the agreement of these data with our morphometric analyses (Mary Sampson unpublished). Additionally, our work complements a monographic study of *Cercidium* and *Parkinsonia* completed by Dr. Julie Hawkins that suggests the possibility of widespread hybridization. At the present time, we agree with Carter (1974a) and Hawkins (1996) that the species are well-delimited entities and should be recognized as separate taxa.

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